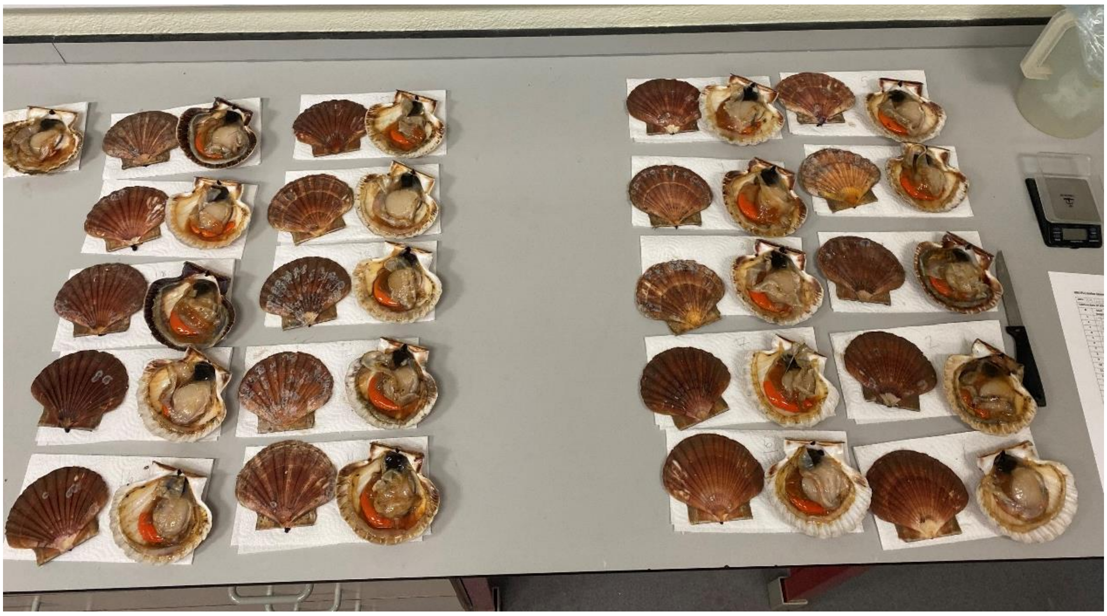
Timing of King Scallop (*Pecten maximus*) Spawning in Devon and Severn IFCA's District



Research Report

v1.0

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Contents

Version control history			
Author/Reviewer	**Date**	**Comment**	**Version**
JS	02/02/2023	Draft report	0.1
JS	20/03/2023	Updated draft	0.2
S Clark	21/03/2023	Review of draft	0.3
N Townsend	28/03/2023	Review of byelaw references	0.4
S Clark	03/04/2023	Review of draft	0.5
JS	14/04/2023	Report finalised	1.0

Acknowledgements

Devon and Severn IFCA is grateful to the divers who provided information and supplied scallops for this project, and also to Mr Kyle Payton, whose assistance in collecting and processing samples for this research was invaluable. Kyle submitted a report based on a subset of the data presented here as his MSc dissertation at the University of Plymouth in 2022.

Cover image: Processing king scallop (*Pecten maximus*) samples caught in Devon and Severn IFCA's District.

Executive Summary

This study investigated the timing of king scallop (*Pecten maximus*) spawning in South Devon between 8th April – 14th October 2022. Approximately weekly during this time, samples of 20 scallops per site were obtained from commercial divers operating in each of the three study sites in Devon and Severn Inshore Fisheries and Conservation Authority's (D&S IFCA) District: Lyme Bay, Torbay, and Start Bay.

Scallops were dissected and three measures of spawning activity were calculated: (i) the gonadosomatic index (GI), (ii) the proportion of mature scallops in a sample, based on the visual appearance of the gonad, and (iii) the proportion of scallops classed as spent or recovering from spawning, also based on the visual appearance of the gonad. The GI describes the gonad (roe) weight as a proportion of total (shell) weight. High GI values are seen in scallops with large gonads (roe) relative to their shell weight; a sharp decrease in the value of GI indicates a decline in gonad condition associated with spawning activity and can therefore be used as an indicator of spawning condition and timing across a season.

In total, 1232 scallops were collected from 58 samples from the three sites. The measures of spawning activity varied substantially throughout the year. The peak in relative gonad weight occurred in early May, then declined steadily throughout the sampling period (to mid-October) as gonad weight decreased relative to total body weight, associated with spawning from early May throughout the summer season. The period in which > 50% of scallops are mature (nearing spawning) in South Devon is likely to range between at least early April and the end of July, but may extend into mid-August. The proportion of scallops classed as spent or recovering increased rapidly from mid-May and peaked between July and September.

The evidence also shows that scallops in a site do not all spawn at one time, that the spawning season may be relatively long, and that there is likely to be fine-scale variation in spawning condition and maturity within sites. This variation can be exploited by some fishers who may target scallops with visually-appealing roe that can command a higher market price due to restaurant demand. This may be possible by changing the depth fished.

Category One Diving Permit Conditions were reviewed in 2022, allowing removal of scallops by commercial divers from specified areas of D&S IFCA's District during July, August and September. The removal of scallops during this period is subject to additional restrictions such as an increase in Minimum Conservation Reference Size from 100mm to 110mm, vessel monitoring, and a bag limit of 2400 scallops per vessel per day. In contrast, a full closed season (1st July to 30th September) remains in place across the District for Category One Mobile Fishing Permit holders. The value of a closed season for scallops depends on the life stage that is intended to be protected and the unique impacts of each fishing method. The evidence suggests that a July–September closed season is likely to protect some individuals in good spawning condition, and overlaps well with the peak in the proportion of individuals classed as spent or recovering. However, this time window is unlikely to protect the majority of individuals during the period when their relative gonad weight is highest, pre-spawning. Impacts of this will depend largely on the quantity of stock harvested by different methods at this time, in addition to mortality of undersize as a result of fishing activity, which is more likely for scallop dredges. Dredges are also less selective of the species and sizes brought on board a fishing vessel. The quantity of stock harvested by the different fishing methods in D&S IFCA's District was assessed in Parkhouse and Stewart (2023).

The landings and spatial footprint of the dive fishery are small relative to the mobile gear fleet. The diving activity can also be more restricted by weather conditions. By contrast, mobile gear fishing can harvest large quantities of scallops and also modify large tracts of seabed, which has the potential to disrupt scallop settlement and development.

1. Introduction

1.1. Background to king scallop fisheries

King scallops (*Pecten maximus*) are the target of some of the most valuable fisheries in the United Kingdom (MMO, 2023), with provisional data for 2022 suggesting a total landings value of over £53 million from all gear types for this species (MMO, 2023), from an estimated 28,410 tonnes of landed scallops. These landings data also demonstrate a clear divide between gear types in terms of landings and value, with dredges and trawls accounting for 97% of all UK landings (95% of value), and the remaining 3% of landings and 5% of value primarily landed by commercial divers (MMO, 2023). Data on the landings by vessels permitted to fish for scallops by diving or using mobile gear in D&S IFCA's District are presented in Parkhouse and Stewart (2023).

The fisheries which prosecute scallop stocks are not subject to nationally- or internationally-set quota or total allowable catch (TAC) restrictions; instead, they are managed via national- and regional-level measures in place via legislation, fishing licence conditions and byelaws. Regional-level management of scallop fishing activity in Devon and Severn IFCA (D&S IFCA)'s District is set out in D&S IFCA's activity-based Permit Byelaws, including the Mobile Fishing Permit Byelaw and the Diving Permit Byelaw, and their associated Permit Conditions.

Nationally and regionally, two key components of king scallop fisheries management have included the Minimum Conservation Reference Size (MCRS) and seasonal closures. MCRSs are the minimum sizes at which the target species can be retained and landed and are set based on the estimated size at maturity, allowing smaller individuals to breed before they are removed by fishers. Seasonal closures for fisheries targeting king scallops typically aim to protect stocks during spawning seasons, in particular by reducing fishing pressure during the spawning season, which is thought to occur between May and October, allowing the remaining stock a chance to spawn as well as increasing protection for juvenile scallops to grow to spawning size and MCRS before encountering scallop gear (Le Pennec *et al.*, 2003; Salomonsen *et al.*, 2015; Lawler and Nawri, 2022).

Both MCRS and seasonal closures have been applied to scallop fisheries in D&S IFCA's District. In 2022, D&S ICA's Byelaw and Permitting Sub-Committee agreed changes to the Commercial Diving Permit Conditions, allowing removal of scallops by commercial divers from specified areas of D&S IFCA's District during July, August and September. The areas from which removal of scallops is allowed are specific Marine Protected Areas where the use of scallop dredges is prohibited year-round. The removal of scallops by diving during July–August is subject to additional restrictions such as an increase in Minimum Conservation Reference Size from 100mm to 110mm, vessel monitoring, and a bag limit of 2400 scallops per vessel per day. A full report on the decision-making process can be read here. In contrast, a closed season (1st July to 30th September) remains in place across the District for Category One Mobile Fishing Permit holders. Similarly, the application of seasonal closures in English waters overall has evolved over time. There is an ongoing need to review such management measures to ensure that they remain effective, including by accounting for possible temporal and spatial variation in the timing of king scallop spawning, as outlined below.

1.2. King scallop reproductive biology

The king scallop is a hermaphroditic species (containing both male and female reproductive parts) which breeds via broadcast spawning (releasing gametes – sperm and eggs – into the water column). Individuals typically release sperm and eggs separately, which may partially avoid self-fertilisation. Fertilisation takes place in the water column, with larval formation generally occurring within 24 hours. Larvae then remain in the water column for 15–32 days

(Le Pennec *et al.*, 2003) before metamorphosing into spat which settle on a range of substrates including erect hydrozoans and bryozoans, attached via byssal threads (Lawler and Nawri, 2022). The pelagic phase, from spawning to spat fall, lasts approximately 18 – 42 days (Le Pennec *et al.*, 2003) during which long-range dispersal is possible, depending on local hydrodynamic conditions. Once spat are around 1-5 mm in size they then settle on the seabed. Growth rates are extremely variable even at small spatial scales, and time to maturity can vary between two to five years; Cefas assumes maturity to be achieved in scallops at 80mm flat shell height (Lawler and Nawri, 2022).

1.3. King scallop spawning behaviour

Across Europe, scallop populations are thought to exhibit low-level 'trickle' spawning throughout spring to autumn (with mature gonads found throughout the year) in addition to one or two peaks of synchronous spawning, which may improve fertilisation rates (Barber and Blake, 2006). As filter feeders, scallops are continuously 'sampling' their environment; by this mechanism, detecting the presence of sperm or eggs in the water is thought to encourage spawning during these synchronous spawning episodes (Barber and Blake, 2006).

The frequency, timing and duration of spawning episodes can vary substantially across small spatial scales, and are determined by a range of factors including internal (e.g. genetic) and environmental factors (e.g. water temperature, food availability) (Le Pennec *et al.*, 2003). For example, in Ireland, the timing of the first spawning event differed by one month between bays separated by a distance of less than 15 miles (Wilson, 1987). In waters off Holyhead (Wales), king scallop spawning exhibits a spring and a summer peak, after which gonads recover rapidly and remain full until the following spring (Baird, 1966). This appears to be typical of most king scallop populations, though one area in Norway and one area in France contain populations in which the gonad was found to not rebuild fully until the following spring (Paulet *et al.*, 1988; Magnesen and Christophersen, 2008). Recovery rates are likely to vary between individuals and with environmental factors, but individuals are thought to be able to recover and spawn again after only one week of conditioning in hatcheries (Le Pennec *et al.*, 2003); recovery rates outside of hatcheries are less clear.

1.4. Aims

The timing of king scallop spawning appears to vary spatially at a range of scales, and with diverse environmental variables, which leads to uncertainty in the efficacy of broadly-applied seasonal closures. Further evidence is required on spawning timing and its variation in king scallops, to inform regionally-appropriate management in D&S IFCA's District.

This study therefore set out to:

(1) quantify the king scallop spawning season in D&S IFCA's District,
(2) identify spatial variation in the timing of that period, and thereby
(3) provide an evidence base to help support the sustainable management of the fishery in D&S IFCA's District

2. Methods

2.1 Data collection

Approximately once a week between 8th April 2022 and 14th October 2022, samples of 20 scallops per site were obtained from commercial divers operating in each of the three study sites in D&S IFCA's District: Lyme Bay, Torbay and Start Bay (Figure 1). Scallops caught represented a random subsample of the catch on the sampling day. The Minimum Conservation Reference Size (MCRS) for dive-caught scallops (*P. maximus*) was 110mm during the period 1st July 2022 – 30th September 2022 (inclusive), but 100mm at all other times during the sampling period. To avoid potential sampling bias associated with a systematic change in the size of sampled scallops, commercial divers involved in this work operated under an exemption from D&S IFCA's Diving Permit Byelaw Conditions which enabled them to continue to land a small number of scallops between 100 – 110 mm, and therefore collect a similar size range of scallops across the entire sampling period. The diver at the Torbay site typically provided scallops > 110 mm in width throughout the sampling period, but from July onwards was requested to provide an additional 10 scallops per sample in the size range 100 – 109 mm. These additional scallops were requested in order to increase the sample size and scallop size range to allow for a statistical test of the potential impact of scallop size on spawning. The data from these additional scallops are not presented here, as analysis has demonstrated that their inclusion introduces a strong sampling bias to the analysis (details available on request from the author). Therefore, all samples remain representative of the fishers' usual catches.

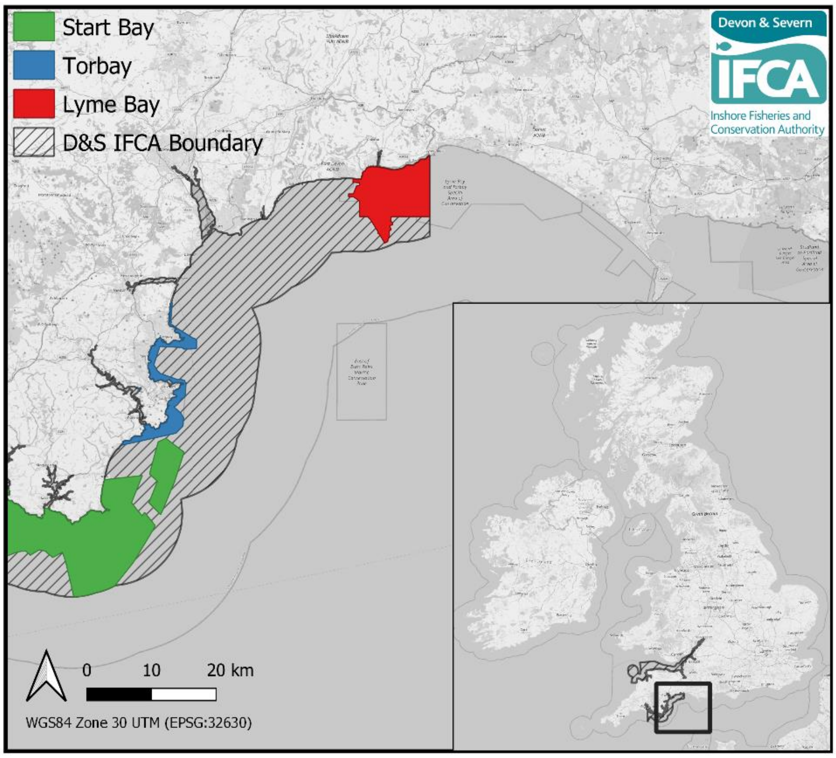

Figure 1. Map of study sites in Devon and Severn IFCA's District: Start Bay, Torbay and Lyme Bay. Study sites were the Marine Protected Areas fished by scallop divers during the study period April – October 2022, in accordance with D&S IFCA's Category One Diving Permit Conditions.

2.2 Sampling Process

The sampling process followed Salomonsen *et al*. (2015) in which scallops were first cleaned of epifauna and sediment, then drained and patted dry to remove excess water. Scallops were then weighed whole to obtain the *shell weight* and the flat shell measured, to the nearest mm, to obtain the shell height and width to the nearest mm (Figure 2a). Each scallop was shucked to remove all soft tissue from the shell. The soft tissue was weighed whole to obtain the *tissue weight*. *Gonad weight* was then obtained by dissecting and weighing the gonad (roe; testis and ovary) after removal of the foot (Figure 2b).

These data were used to calculate the *gonadosomatic index* (GI) (equation 1), which describes the gonad weight as a proportion of total (shell) weight. High GI values are seen in scallops with large gonads (roe) relative to their shell weight; a sharp decrease in the value of GI indicates a decline in gonad condition associated with spawning activity and can therefore be used as an indicator of spawning condition and timing across a season (Salomonsen *et al.*, 2015).

$$GI = \frac{Weight\ of\ gonad}{Shell\ weight} \qquad \text{(Eq. 1)}$$

The stages of gametogenesis (production of sperm and eggs) in adult scallops give rise to a series of macroscopic changes to the appearance of the scallop gonads; these changes can be used to assign a "maturity" stage to each hermaphroditic gonad (Mason, 1958). which are divided into contiguous male and female parts. For this study, each gonad was assigned a maturity stage based on the macroscopic visual appearance descriptors outlined in Mason (1958) (Table 1; Figure 3).

Scallops were processed fresh wherever possible, but frozen and later thawed for processing in 26% of cases. Freeze-thaw trials indicated there was no discernible difference in GI or maturity values between samples whether processing occurred with fresh or thawed scallops (Salomonsen *et al.*, 2015; J. Stewart, *pers*. *obs.*).

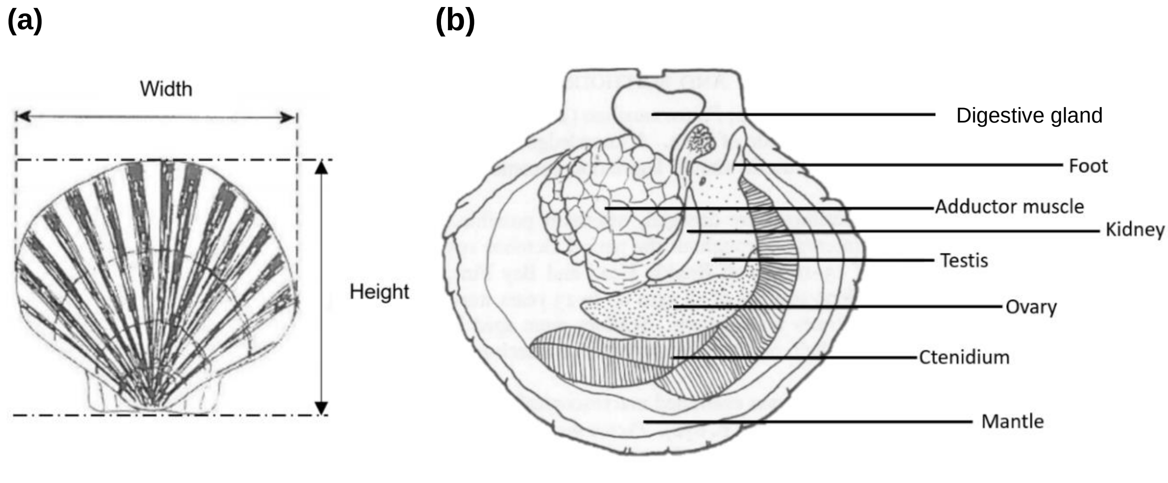

Figure 2. (a) Visual depiction of king scallop height and width measurements used for this study. (b) Internal anatomy of an adult king scallop, adapted from Mason (1958).

Table 1. Gonad maturity stages 1 – 7 based on visual appearance; adapted from Mason (1958).

Gonad stage	Description
0: Immature (virgin)	Gonad small, flat and angular, transparent and colourless. No reproductive tissue visible to naked eye. Whole of loop of alimentary canal clearly seen.
1: Developing (virgin) or spent-recovering (juvenile)	Gonad growing, still flat and angular. Reproductive tissue now visible as minute follicles, translucent and sparse. Gonad uniformly fawn-coloured; no visible differentiation into testis and ovary. Alimentary canal visible.
2: Differentiated gonad (virgin and juvenile)	Gonad growing, still flat and angular, now obviously differentiated into testis and ovary; male follicles white and female fawn or light salmon orange, colour imparted by contents. Follicles still small and sparse and alimentary canal still visible.
3: Recovering	Gonad larger and proportionately thicker, angular. Flabby, containing free water, especially in adults after spawning. Assuming brighter colour, testis white and ovary bittersweet orange. Follicles larger and denser, but still spaces between them, and alimentary canal still visible.
4: Filling	Gonad still larger and thicker (thickness about a third of width); still somewhat flabby, containing a little free water. Outline less angular, but not completely smooth. Colouring brighter due to denser colouring of follicles, testis white, ovary bittersweet orange or grenadine pink. Follicles larger and closer together, the latter, especially in ovary. Alimentary canal still visible between follicles in testis, but not in ovary, but its outline still discernible owing to thinness of gonad.
5: Half full	Gonad again larger and thicker, firmer and containing very little free water. Rounded, with tapering tip. Brighter, testis creamy-white, ovary grenadine pink or grenadine. Follicles larger, becoming packed together. Loop of alimentary canal no longer clearly visible, but still causes wall of gonad to bulge.
6: Full	Gonad is now at its largest, thickest (thickness about half the width) and firmest, containing no free water. Rounded to tip. Bright, with follicles highly coloured and closely packed; testis cream coloured, ovary usually grenadine. Loop of alimentary canal indiscernible.
7: Spent and partially spent	Spawning may be partial or complete. Gonad dull, angular, thin and collapsed; flabby, containing much free water. Spent gonad fawn-coloured and loses visible differentiation into testis and ovary after spawning for the first time. Older scallops usually retain differentiation, testis yellowish-brown, ovary dull orange pink. Follicles appear empty. Partially spent gonad retains differentiation; testis yellowish white, ovary a dull orange. Follicles appear hollow, with a coloured ring around periphery indicating retention of some genital products.

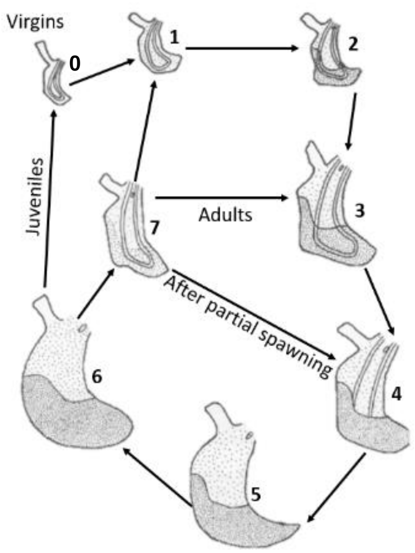

Figure 3. Visual depiction of macroscopic changes in adult king scallop gonad during gametogenesis; stage descriptions available in Table 1 (adapted from Mason, 1958).

2.3 Data analysis

Summary statistics were calculated and plotted for each site including scallop numbers, weight and width. Differences between sites in scallop width and shell weight were tested for using Kruskal-Wallis tests combined with post-hoc Dunn's tests. R v4.1.1 or later (R Core Team, 2021) was used for all data analyses.

2.3.1 Modelling GI

Then, statistical models known as Generalized Additive Models (GAMs) were used to look for evidence that the possible predictor variables day of year, site, scallop height and scallop width could explain the variability in GI over the sampling period. Specialist information on the use of GAMs is given in Appendix 1. Each site was then modelled separately due to subtle differences in GI between sites that warranted further exploration. See Appendix 1 for details of model fitting, selection and diagnostics, which were used to decide upon the most appropriate model for the data for each response variable.

2.3.2 Assessing scallop maturity

Scallop maturity was assessed based on the maturity classifications of Mason (1958) (Table 1). Using the maturity classifications for each scallop, the proportion of mature scallops in each sample was calculated, to give a proportional maturity index. Due to limited uncertainty in the boundaries and transition between maturity stages 5 and 6, the proportion mature was calculated as the proportion of scallops per sample that were in either stages 5 or 6. This approach is reasonable as scallops in stages 3 and 4 are not sufficiently developed to spawn, whereas those in stage 7 are spent. The proportion of 'spent' scallops in each sample was also calculated, based on the proportion per sample that was classified as stage 7 or 3.

Whereas the GI data were modelled with a single value per scallop, each value of the proportion mature and proportion spent indices relates to a sample of scallops (i.e. one index value per sampled fishing trip at each site, e.g. one index value per 20 scallops).

Linear models were used to look for evidence that variation in the proportion of mature scallops in each sample could be explained by day of year and site. This included looking for relationships between maturity and day of year that could be explained by a straight line (e.g. maturity either increases or decreases at the same rate over time), or by a more complex relationship (e.g. maturity could increase at one point in the year then decrease later in the year). Scallop width and height were not considered in these models because the indices are only available at the sample level, not at the level of individual scallops. See Appendix 1 for details of model fitting, selection and diagnostics, which were used to decide upon the most appropriate model for the data for each response variable.

2.4 Additional methods

D&S IFCA Officers conducted a review of the effort and landings of the scallop dive fishery during 2022, in addition to circulating a questionnaire to Category One Diving Permit holders to seek their views on the increased access to scallop stocks during July-September 2022. This additional work is presented in a separate Officer report (Parkhouse and Stewart, 2023), but the results of that work were used to inform the interpretation of patterns observed in the scallop spawning data presented here.

3. Results

Aside from brief summary statistics, the results presented here are shown as figures for ease of interpretation. The underlying tables of statistics are available in Appendix 2.

3.1. Summary of scallop samples

A total of 1232 scallops were collected across 58 samples from the three study sites during the sampling period (8th April 2022 – 14th October 2022). Table 2 summarises the number of scallops collected from each site, in addition to summary statistics on the collected scallops.

Table 2. Summary statistics for scallops sampled from each of three sites 8th April – 14th October 2022. Shell weight was measured after removing epifauna and draining water from scallops.

Site	Number of samples	Number of scallops	Width (mm)		Mean Height (mm)	Mean Shell Weight (g)	Mean Gonad Weight (g)
			Mean	Range			
Lyme Bay	20	402	111.6	98† – 134	96.7	161.9	6.63
Start Bay	22	471	113.5	100 – 137	96.9	172.6	6.72
Torbay	15	310	120.7	104 – 141	104.3	202.5	8.66

† See section 3.2.

3.2. Scallop width and weight comparisons

The scallops sampled ranged from 98 – 141 mm in width (Figure 4). The small number of scallops < 100 mm width showed evidence of chipping of brittle shells, likely during transport after sample collection (J. Stewart, *pers. obs.*); these scallops would have been approximately 100–101 mm in true width. The scallops sampled ranged from 101 – 313 g in total shell weight (Figure 4). Shell weight was measured after removal of epifauna and excess water; therefore, the shell weights presented in Table 2 and Figure 4 cannot be straightforwardly used to convert wet landings weight from MMO landings data into a measure of the number of scallops per landings.

The width and shell weight of sampled scallops differed significantly between sites during the sampling (Figure 4, Table 2, Table 3). All sites were significantly different from one another, with scallops from Torbay being on average larger and heavier than other sites, and those from Lyme Bay being on average smaller and lighter than other sites (Figure 4, Table 2, Table 3).

Table 3. Results of Dunn's test for differences in scallop width and shell weight between sites. p values < 0.05 indicate a significant between-site difference. Dunn's tests were carried out following significant Kruskal-Wallis tests for overall differences between sites.

Comparison	Test statistic (*Z*)	p-value
Width differences between sites		
Lyme Bay - Start Bay	-3.23	0.0012
Lyme Bay - Torbay	-15.99	< 0.001
Start Bay - Torbay	-13.53	< 0.001
Shell weight differences between sites		
Lyme Bay - Start Bay	-4.51	< 0.001
Lyme Bay - Torbay	-15.72	< 0.001
Start Bay - Torbay	-12.06	< 0.001

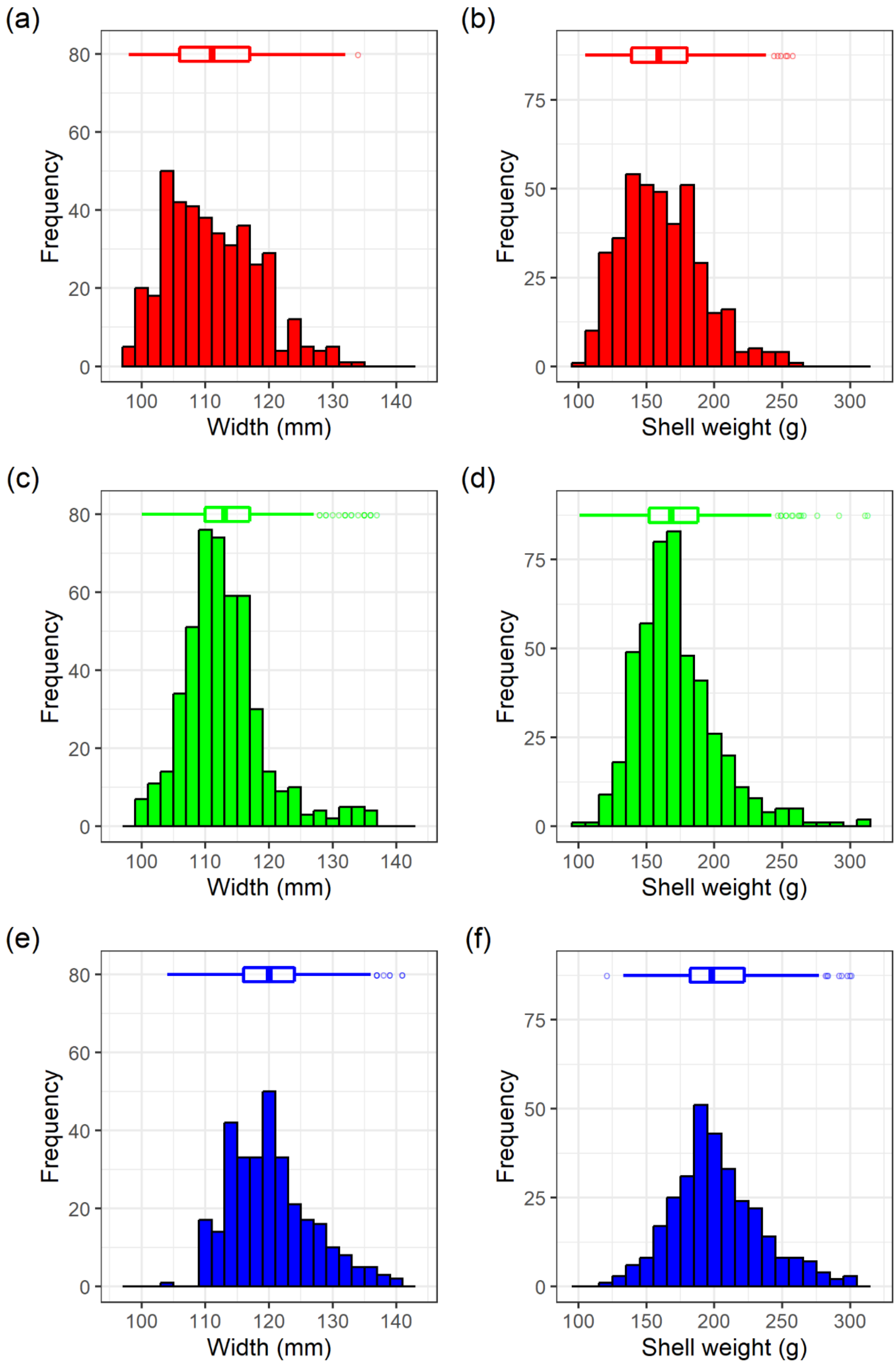

Figure 4. Frequency histograms of width (mm; a, c, e) and shell weight (total weight, grams; b, d, f) of all scallops sampled from Lyme Bay (red), Start Bay (green) and Torbay (blue), with accompanying box and whisker diagrams displaying median, lower and upper quartiles, range and 'outliers'.

3.3. Gonadosomatic index

The GAM modelling (see Appendix 1.1 for details) shows a strong relationship between gonadosomatic index (GI) and day of year (Figure 5): GI appears to peak around day 127 (May 7th), demonstrating that scallops appear to be in peak spawning condition from early May. The relationship (trend line in Figure 5) does not level off until early October, suggesting some spawning activity occurs throughout the summer season. Despite a strong modelled relationship between GI and day of year, Figure 5 also demonstrates that there are likely to be within- and between-site differences in scallop spawning state, with not all scallops spawning at one time, and there can be relatively high variation in GI over the course of a few days even within one site (note variation in coloured circles representing the underlying data; Figure 5).

From the peak in early May, GI then declines steadily throughout the sampled period (to mid-October) as gonad weight decreases relative to total body weight, associated with spawning (Figure 5). There is also a very weak effect of scallop width, particularly in the Lyme Bay samples: gonad weight tends to be smaller relative to total body weight in smaller scallops than in larger scallops (Figure 6) (Appendix 2.1.1).

The model shown in Figure 5 indicates the relationship between GI and day of year across South Devon. Due to apparent differences in the underlying data, the relationship between GI and day of year was also modelled separately for each site (Figure 7), which appears to indicate a different pattern of spawning condition across the year in Lyme Bay compared to the other sites; the model for Lyme Bay also explained a lower proportion of the "deviance" (i.e. explained less of the variation in the site-specific data) than models for other sites (Table A2.2, Appendix 2.1.2). The reasons for these patterns are explored in the Discussion (section 4.2). The site-by-site modelling demonstrated that scallop width was not useful as an additional predictor of variation in GI, and that patterns of variation in GI were best explained simply by day of year (Appendix 2.1.2).

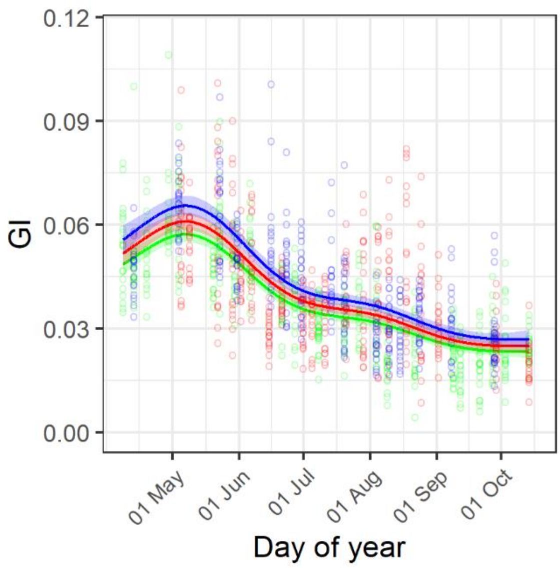

Figure 5. Relationship between Gonadosomatic Index (GI) and day of year across three sites: Lyme Bay (red), Torbay (blue) and Start Bay (green), superimposed on raw data values for each scallop and sampling day. Also shown are 95% confidence intervals (coloured ribbons), which indicated high certainty in the shape of the modelled relationship between GI and day of year.

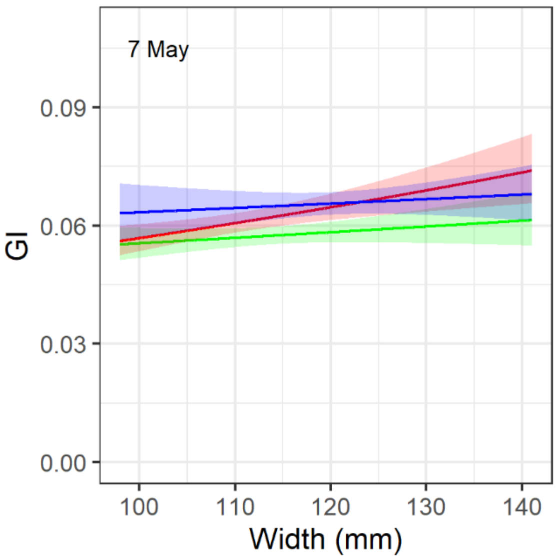

Figure 6. Weak relationship between scallop gonadosomatic index (GI) and width (mm) for three sites: Lyme Bay (red), Torbay (blue) and Start Bay (green). GI also varies with day of year (see), so the GI-width relationship has been plotted here for 7th May, identified as the GI peak across those sites. The GI-width relationship appears to be more pronounced for Lyme Bay, where a greater number of small scallops were sampled. Also shown are 95% confidence intervals, (coloured ribbons) which demonstrate a large amount of uncertainty in the modelled relationship between width and GI.

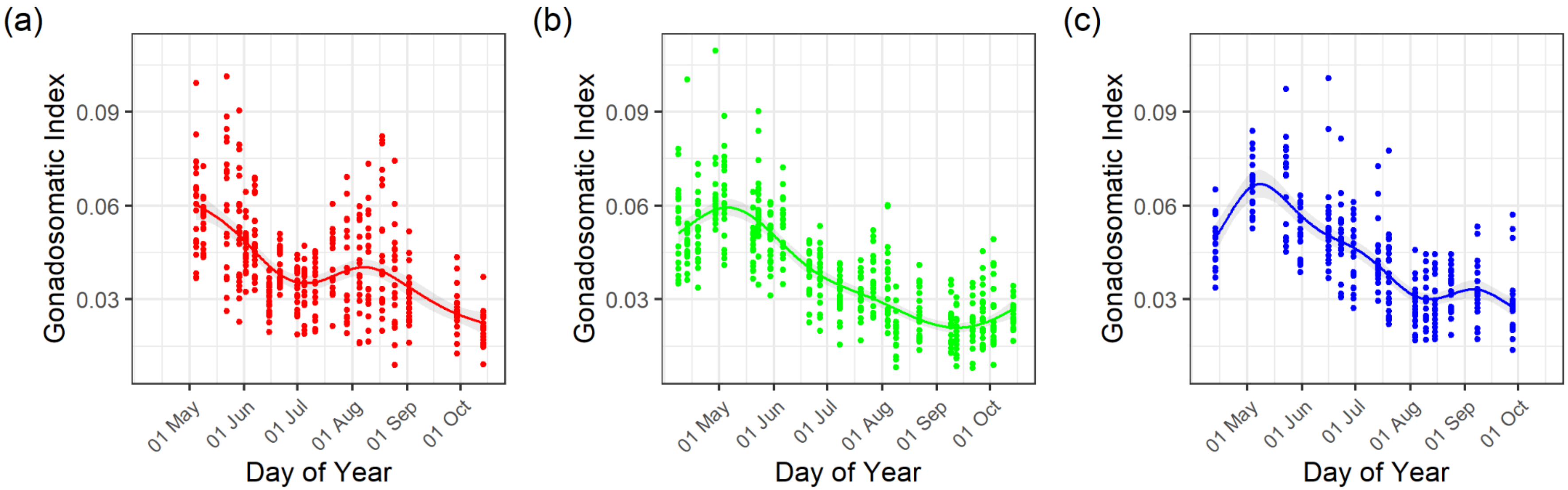

Figure 7. Relationship between Gonadosomatic Index and day of year when modelled separately for each site: Lyme Bay (red), Start Bay (green) and Torbay (blue). Also showing 95% confidence intervals (grey ribbon) around the modelled relationship, superimposed on the underlying data (coloured points).

3.4. Maturity indices

The proportion of scallops classed as being mature (in maturity stages 5 and 6) appeared to peak around day 150 (May 30th), though the confidence intervals are relatively wide (grey ribbon, Figure 8a), suggesting the peak could have occurred earlier or slightly later. Shortly after this peak, the proportion classed as spent or recovering increased relatively rapidly, to a peak at day 250 (September 7th). Again, there are wide confidence intervals so the peak in the proportion classed as spent/recovering could have occurred as early as August 12th or as late as October 14th (Figure 8b).

The period when > 50% of sampled scallops were mature (in maturity stages 5 and 6) ranged between approximately day 110 and day 201 (April 20th – July 20th). There is some uncertainty around this estimate as shown by the 95% confidence intervals in Figure 8a; therefore, the period in which more than 50% of scallops were mature could have occurred in the narrower window of April 21st – July 7th, or the broader window of early April – August 3rd, with greatest certainty around the range April 20th – July 20th. After the peak in proportion mature, an increasingly greater proportion of scallops were in maturity stages 7 (spent), 3 (recovering) and 4 (filling).

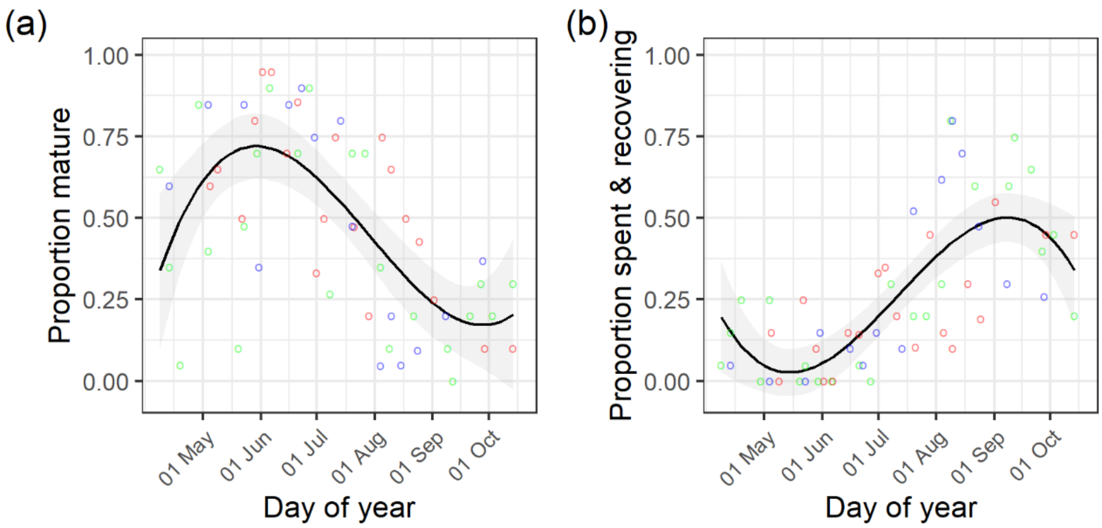

Figure 8. Proportion of each sample of scallops (n = 58) that was (a) mature (stages 5 or 6) and (b) spent and recovering (stages 7 or 3). There was no difference in proportion mature between sites, but the peak in proportional maturity at Lyme Bay (red line, figure b) was slightly lower than other sites (blue and green lines, figure b). Also displaying 95% confidence interval (ribbons) and underlying data (coloured circles). The proportion of scallops classed as being mature peaked around day 150 (May 30th), those classed as spent or recovering increased rapidly from this date and peaked around day 250 (7th September). Underlying statistics available in Appendix 2.2.

3.5. Summary of spawning timing

Table 4 summarises the estimated timing of spawning based on the metrics outlined above.

Table 4. Visual summary of estimated timing of spawning based on gonadmosomatic index (GI) and maturity indices.

<table>
<tr><th>April</th><th>May</th><th>June</th><th>July</th><th>Aug</th><th>Sept</th><th>Oct</th></tr>
<tr><td></td><td>Largest GI – Peak in roe size (pre-spawning)</td><td colspan="5">Steady decline in GI due to spawning</td></tr>
<tr><td colspan="4">Over 50% of scallops have large roes that are near spawning condition</td><td colspan="3"></td></tr>
<tr><td colspan="2"></td><td colspan="3">Increasing numbers of scallops are spawning and seen in post-spawning condition (spent /recovering).</td><td colspan="2"></td></tr>
<tr><td colspan="3"></td><td colspan="3">July – September period has some scallops with full roe (July) and overlaps with majority of scallops spawning</td><td></td></tr>
</table>

4. Discussion

This study used fishery-dependent sampling to assess the timing of scallop maturity and spawning in South Devon. As outlined below, it has identified key time periods during which contribution to the local spawning potential may be at its highest. In this discussion, section 4.1 discusses the implications of variation in the sizes and weights of scallops sampled; section 4.2 considers the variation in gonadosomatic index in South Devon and its potential management implications, and section 4.3 considers the variation in scallop maturity in South Devon and its potential management implications. Section 4.4 then considers management implications overall in the context of the different fisheries that prosecute scallop stocks in south Devon.

4.1 Variation in scallop size and weight

Although the sizes and weights of sampled scallops differed between sites in this study there is not sufficient evidence to indicate whether this is representative of the scallops available on the ground in each site. Thorough transect surveys using divers or towed cameras would be required to validate this. Anecdotal evidence suggests that, instead, these differences between sites may result from a sampling bias associated with the fishery-dependent nature of the sampling. The scallops sampled were requested to be a representative sample of the typical catch, and some fishers (including those in Start Bay and Torbay who participated in this project) are known to target larger scallops due to a self-imposed minimum size that is larger than the Minimum Conservation Reference Size. Although there were significant differences in scallop width and weight between sites, it is considered beneficial to have been able to sample a wide range of sizes (and therefore ages) of mature scallops, to gain a robust estimate of the spawning season timing.

Furthermore, though the fishery-dependent nature of this study may have introduced a slight sampling bias regarding scallop size, the remaining analyses are robust to this. First, there does not appear to be a strong relationship between scallop size and variation in the gonadosomatic index (GI), at least for the size range of scallops sampled here. The strongest potential relationship was identified for Lyme Bay (Figure 6), where most of the smaller scallops (100 – 110 mm width) were sampled; however, there is a large amount of uncertainty in this modelled relationship, suggesting no clear width-GI relationship. Given that scallops become mature after a given size (assumed by Cefas to be 80mm flat shell height; Lawler and Nawri, 2022), it is possible that some of the smaller scallops were unable to obtain a higher GI value compared to the larger scallops, but that after a given size/age the relationship between GI and size may level off. Secondly, GI is calculated using gonad weight as a proportion of shell weight, so scallop weight (and, by proxy, size) is controlled for in this way. Finally, the modelling approach used here had the potential to include width as a predictor of GI, so it was possible to control for the effect of scallop width on GI. Width was also not identified as an important predictor of scallop maturity, or of scallop GI when modelled site-by-site. In summary, inter-site variation in the size of sampled scallops is unlikely to have introduced important bias to the results presented here.

4.2 Variation in gonadosomatic index

Gonadosomatic index (GI) values showed a clear peak in early May, which indicates this was the approximate time at which scallops in South Devon were in their peak spawning condition (gonad weight is highest relative to shell weight) (Figure 5). GI then declined relatively sharply as increasing numbers of scallops spawned and their gonads (roes) became relatively lighter and changed appearance from large, firm and brightly coloured to smaller, dull and flabby. Therefore, if there is interest in managing scallop stocks by increasing the spawning potential of the stock, a potentially useful target window for protection could include the peak in spawning condition in early May, and a window around that time when individuals are preparing to spawn and actively spawning. It is important to note that spawning activity appears to continue throughout the sampled period, with the decline in spawning condition not levelling off until early October, which indicates that a larger proportion of scallops are beginning to build up their gonadal tissue again.

GI values were also assessed on a site-by-site basis (Figure 7). This assessment appears to indicate that there was a second partial peak in spawning condition (relative gonad size; GI) in Lyme Bay in early-mid August (Figure 7), though the site-specific model for Lyme Bay explains less of the variation in the data than do the site-specific models for other sites, indicating that day of year is a less robust predictor of trends in GI for Lyme Bay (Table A2.2, Appendix 2). There also appears to be an increase in the variability of individual scallop GI values in Lyme Bay and Torbay, indicated by the “fanning out” of the underlying GI values shown in Figure 7. This may suggest that a proportion of the scallops sampled had fully spawned (relatively lightweight gonads), others had partially spawned (and retained relatively heavy gonads), while others were still pre-spawning (with full gonads). However, data collected by Parkhouse and Stewart (2023), suggest a different explanation. Some buyers of scallops prefer to buy and sell scallops with roe (gonads) in good condition, in part because they present better when served to customers. The diver in Lyme Bay, where a potential second peak in spawning was most apparent, indicated that it is possible to move areas when diving in order to target scallops with roe in better condition, for example by diving in deeper waters where the spawning may occur later in the year. The iVMS data for this vessel indicate that the vessel moved fishing location at the same time of year at which the second apparent peak in GI occurred (data not shown). This highlights two important points: firstly, there may be substantial fine-scale spatial variation in the timing of spawning, in which spawning (which is at least partially temperature-dependent) occurs later in deeper waters. Therefore, the fishery-dependent sampling used in this project may not have completely captured the range of spatial variation in timing of spawning. Further evidence for fine-scale variation in timing of spawning comes from the clear variation in GI values between samples at each site (coloured circles in Figure 5). Previous studies of the timing of scallop spawning at other locations have found relatively high variation in timing over small spatial scales (e.g. Wilson, 1987). Secondly, fisheries capable of targeting waters of varying depth can, at least in some cases, adjust their fishing practices to target stocks in peak spawning condition, which may have implications for potential protection of spawning stock.

4.3 Variation in scallop maturity

The analysis of proportional maturity in sampled scallops suggested that the peak in readiness to spawn occurred at the end of May, then declined as increasing numbers of scallops spawned (Figure 8a). This peak is slightly later than the estimate provided by assessment of GI values: this may be because the proportional maturity included both maturity stages 5 and 6 in the calculations. However, the uncertainty around the estimate (Figure 8a) also indicates that the peak in readiness to spawn (based on proportional maturity) could have occurred earlier, better coinciding with the estimate of peak spawning condition based on GI. This uncertainty is partly due to the high variation in maturity index values between samples even within sites. The coloured circles in Figure 8a demonstrate that the proportion of scallops that are in peak condition sometimes varies greatly week-to-week.

The period in which > 50% of scallops are mature in South Devon is likely to range between at least mid-April and mid-July. This period encompasses the peak of spawning condition assessed based on GI at all sites (Figure 5). Therefore, if there is interest in managing scallop stocks by increasing the spawning potential of the stock, a potentially useful target window for protection could include this period, during which a large number of individuals are preparing to spawn and spawning. The proportion of scallops classed as spent and recovering increased rapidly from the end of May to peak in early September (although the statistical uncertainty in this estimate suggests the peak could have occurred as early as August 5th, or later in September. This indicates widespread active spawning occurred in D&S IFCA's District in between the end of May and end of September, with little widespread recovery seen by the end of the sampling period in mid-October.

This study used three different methods to assess the timing of scallop spawning in South Devon: the GI method, proportional maturity method and proportion spawned method. The GI method was based on easily-measured weights and is therefore a highly objective assessment tool. By comparison, elements of the maturity assessments were relatively subjective, depending on visual assessments of the appearance of scallop gonads which could occasionally be difficult to reliably categorise. Therefore, the GI assessment likely provides a more reliable estimate of the timing of peak scallop spawning condition (relative gonad weight) and how this changes during spawning activity, but the combination of the three approaches provides a robust assessment of the period in which scallops are spawning in South Devon.

4.4 Management implications of scallop spawning timing

The scallop closed season for D&S IFCA Category One Diving Permit holders previously applied across the District. In 2022, the relevant Permit Conditions were amended, allowing removal of scallops by commercial divers from specified areas of D&S IFCA's District during July, August and September, subject to additional restrictions such as an increase in Minimum Conservation Reference Size from 100mm to 110mm, vessel monitoring, and a bag limit of 2400 scallops per vessel per day. A District-wide seasonal closure (1st July – 30th September) remains in place for mobile gear under the conditions of the Category One (at sea) Mobile Fishing Permit Byelaw.

Seasonal closures have been used as a fisheries management tool in a range of scenarios; for scallops, the protection afforded by a closed season could include protection of a spawning stock, protection of a stock that is recovering from spawning, and protection of the surrounding habitat to allow settlement and development of juvenile scallops. Due to the nature of scallop development, the value of implementing a closed season with the intention of protecting settled and developing spat will depend largely on the nature and impacts of the fishing activity concerned. The nature of the activity of fishing for scallops by diving is unlikely to have an impact on the substrate, settled spat or undersize scallop, as there is minimal disturbance of the substrate by divers or their gear. This is in contrast to the activity of fishing for scallops using dredges, which can disturb large tracts of seabed with potential impacts on scallop settlement and other biodiversity (Stewart and Howarth, 2016). This is a key difference between the fishing methods and their potential for impacts on scallop stocks. In scallops, spat fall occurs approximately 18 – 42 days after spawning (Le Pennec *et al.*, 2003). During settlement, the young scallops attach by byssal threads to the substrate (e.g. seaweed, clean shell, bryozoans, hydroids and sediment) until they are large enough to detach and become free-swimming. Detachment occurs once scallops reach between 4-13mm in width, which would occur within their first year of growth. After detachment, they settle on the seabed but are capable of free-swimming behaviours, for example in predator avoidance. Young scallops swim readily but fatigue quickly, so only move short distances at a time. Consequently, spat and young scallops may be vulnerable to passes of mobile fishing gear despite being below the MCRS. Dredge impacts to possible settlement substrates also negatively impact scallop recruitment by damaging or destroying available settlement locations, while protection of such “nursery areas” can improve recruitment (Howarth and Stewart, 2014).

As highlighted above, further reasons for implementing a closed season as a fishery management tool could include protection of a spawning stock or protection of a stock that is recovering from spawning. The evidence presented here suggests that a July–September closed season is likely to protect some mature individuals in good spawning condition during those months, and overlaps well with the peak in the proportion of individuals classed as spent or recovering – and therefore with much of the peak of spawning activity itself. However, this time window is unlikely to afford protection to the majority of individuals in peak spawning condition, because relative gonad weight (spawning condition) peaks in early May onwards. Potential impacts of this will depend largely on the quantity of stock harvested by the different methods between May and end of June (and how much is left *in situ* able to spawn), in addition to the lethal and sub-lethal impacts on undersize scallops as a result of fishing activity, which is known to be more likely for mobile gear (e.g. Howarth and Stewart, 2014; Stewart and Howarth, 2016). The quantity of stock harvested by the different fishing methods in D&S IFCA’s District was assessed in Parkhouse and Stewart (2023), who compared the landings of dive-caught scallops in D&S IFCA’s District in 2022 to dredge-caught landings from ICES area 27.VIIe to the ports of Brixham, Exmouth, Teignmouth, Plymouth and West Bay. West Bay was included due to its inclusion in the dive vessel landings. Dredge landings were based on 2019 data, the last year for which data were available at the time of analysis. Parkhouse and Stewart (2023) found that dive-caught scallop landings in 2022 were only approximately 5% of the landings from the scallop dredge fleet in 2019, highlighting the large difference in likely impact on stocks between the methods. In addition to the impact of direct removals, evidence from other marine mollusc species suggests that high fishing effort can reduce fertilisation success and truncate age structures, leading to poor recruitment and reductions in scallop population density (Macleod *et al.*, 1985; Stoner and Ray-Culp, 2000; Vause *et al.*, 2006).

5. Conclusions

The majority of scallops in South Devon are likely to reach maturity and peak spawning condition (high relative gonad weight) between April and late July. Active spawning behaviour appears to increase from late May and peak in late August/early September. The timing of a 1st July – 30th September scallop closed season therefore appears to miss the peak of spawning condition for the majority of scallops in D&S IFCA’s District, but appears to protect a large portion of the stock that is actively spawning and beginning to recover between May and September. This closure is in place throughout the District for Category One Mobile Fishing Permit holders and throughout the District except in specified areas under specific conditions for Category One Diving Permit holders. The value of this closure may depend on the fishing pressure on the mature pre-spawning individuals, the intensity of which may influence the proportion of mature individuals that survive to spawn. The closed season for mobile gear fishers in D&S IFCA’s District may have additional value in protecting some of the scallop spat that are beginning to settle on the substrate prior to their development into a free-swimming life stage.

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Appendix 1: Supplementary information on methods for Devon and Severn IFCA Research Report '*Timing of King Scallop (Pecten maximus) Spawning in Devon and Severn IFCA's District*'

Appendix 1.1. Generalised Additive Models (GAMs) of Gonadosomatic Index (GI)

A Generalised Additive Model (GAM) is a modelling technique in which the impact of predictor variables (e.g. day of year) on the response variable (e.g. gonadosomatic index) is described by smooth functions which can be non-linear, i.e. rather than describing a straight-line relationship between a predictor and response variable, the relationship can be described as a smooth curve. The smooth function for each variable is non-parametric; that is, it is defined by the data rather than by a set of parameter estimates. The shape of curves that are fitted through the data are defined by a number of curve inflection points ("knots"), the number and position of which are defined using a 'maximum likelihood' approach during model estimation using R package 'mgcv' (Wood, 2017, 2023).

GAMs were applied to test predictors for the gonadosomatic index, including data from all sites. GI was also modelled for each study site independently, due to subtle differences in GI between sites that warranted further exploration on a site-by-site basis. All plausible combinations of predictors (for which data were available) and their two-way interactions were considered, from the following: day of year, scallop width and scallop height. Site identity was included as a possible predictor for all GAMs which included data from all sites (i.e. those GAMs tested for a difference in the predictor variable between sites). All GAMs were based on beta errors using a logit link.

As the smooth functions for each predictor variable are non-parametric, the effect of a predictor variable on each response is interpreted based on its inclusion and significance in the final model for each site, and on the graphical plot of the effect, rather than based on a set of parameter estimates (as would be the case with linear models). Therefore, numerical model outputs are included only in the Appendix here, rather than in the main text, for ease of interpretation.

As outlined above, the optimum number of 'knots' in the GAM smooth function for each predictor variable was defined using a maximum likelihood approach during model estimation. However, to avoid overfitting, the final GAM for each response variable was re-estimated using pre-defined numbers of knots between 1 (indicating a linear relationship between predictor and response variables) and *n*, where *n* is the 'optimum' number of knots defined during model estimation. These re-estimated GAMs were compared to the previously-estimated final model for each response variable, using the model selection approach below (Appendix 1.3) to define the most parsimonious model in each case.

Simpler general(-ised) linear modelling approaches (with beta or binomial errors according to the underlying distribution of the response data) were considered for modelling putative predictors of GI. However, these approaches resulted in poor model diagnostics using standardised simulated residuals generated using R package "DHARMa". Therefore, the GAM approach described above was used.

Appendix 1.2. Linear Models of Maturity Data

Scallop maturity was assessed based on the maturity classifications of Mason (1958) (Table 1, main text). Using the maturity classifications for each scallop, the proportion of mature scallops in each sample was calculated, to give a proportional maturity index. Due to limited uncertainty in the boundaries and transition between maturity stages 5 and 6, the proportion mature was calculated as the proportion of scallops per sample that were in either stages 5 or 6. This approach is reasonable as scallops in stages 3 and 4 are not sufficiently developed to spawn, whereas those in stage 7 are spent. The proportion of 'spent' scallops in each sample was also calculated, based on the proportion per sample that was classified as stage 7 or 3.

Whereas the GI data were modelled with a single value per scallop, each value of the proportion mature and proportion spent indices relates to a sample of scallops (i.e. one index value per sampled fishing trip at each site, e.g. one index value per 20 scallops).

Linear models (Gaussian error structure, identity link function) were used to look for evidence that variation in the proportion of mature scallops in each sample could be explained by day of year and site. This included looking for relationships between maturity and day of year that could be explained by a straight line (e.g. maturity either increases or decreases at the same rate over time), or by a more complex relationship (e.g. maturity could increase at one point in the year then decrease later in the year). Scallop width and height were not considered in these models because the indices are only available at the sample level, not at the level of individual scallops. The same approach was taken to look for evidence that variation in the proportion of spent scallops in each sample could be explained by day of year and site. For models of proportion mature and proportion spent, log link functions were also tested, but models with identity link functions were deemed to be the most parsimonious. See Appendix 1.3 for details of model fitting, selection and diagnostics, which were used to decide upon the most appropriate model for the data for each response variable.

Appendix 1.3. Model fitting, selection and diagnostics

For each response variable, a candidate set of models that were consistent with the data was generated. AIC (Akaike Information Criterion) was used as the criterion to select among these candidate models. The lowest AIC model is likely to be the most parsimonious, but AIC is only an estimate of parsimony. Therefore, following Richards (2008) and Henly *et al.* (2021), certain other models were also considered. First, a candidate model set was developed which had AIC values within 6 AIC units of the lowest AIC value among models. Then, to prevent unsupported, overly-complex models being selected, models were removed from the candidate set if they were more complex versions of other selected models (Richards, 2008, 2015; Henly *et al.*, 2021). In cases when this process did not identify a single 'best' model, biological inference was based on the model with fewest terms (or lowest AIC where models had the same number of terms), following Richards (2015). This approach identified a single 'final model' in each case.

Variance inflation factors were used to ensure a lack of significant collinearity amongst predictors in all final models (Zuur *et al.*, 2010). Model diagnostics were assessed using standardised, simulated residuals, generated using the R package 'DHARMa' (Hartig and Lohse, 2020).

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Appendix 2: Supplementary information on results for Devon and Severn IFCA Research Report '*Timing of King Scallop (Pecten maximus) Spawning in Devon and Severn IFCA's District*'

Aside from brief summary statistics, the results presented in the main text are shown as figures for ease of interpretation. This appendix shows numerical details of the underlying statistics.

Appendix 2.1. Numerical GAM results

This section outlines the model selection (AIC analysis for choosing the most parsimonious model) and parameter estimates for the Generalised Additive Models (GAMs) which were used to assess predictors of the Gonadosomatic Index (GI), both across the District (Appendix 2.1.1) and on a site-by-site basis (Appendix 2.1.2).

Appendix 2.1.1. Numerical GAM results: District-wide Gonadosomatic Index

The GAM modelling (see Appendix 1.1 for details) shows a strong relationship between gonadosomatic index (GI) and day of year (Figure 5, main text), alongside within- and between-site variation in GI. There is also a very weak effect of scallop width, particularly in the Lyme Bay samples: gonad weight tends to be smaller relative to total body weight in smaller scallops than in larger scallops (Figure 6, main text).

The model shown in Figure 5 and Figure 6 (main text) was chosen as the most parsimonious following the model selection methods outlined in Appendix 1.3. A summary of AIC analyses for this modelling is shown in Table A2.1.

Table A2.1. Summary of AIC analyses for District-wide models of gonadosomatic index. Inclusion of the predictors "s(Day)" (smooth term for day of year), Site, "Width" (scallop width) and the interaction between site and width ("Site:Width") is denoted by ● for relevant models. Other putative predictors (e.g. scallop width) were tested but not deemed important after AIC-based model selection (Appendix 1.3). The final model (denoted $_{FINAL}$) includes only those predictors that were deemed to be significantly associated with variation in the gonadosomatic index. Also shown are the number of knots (curve inflection points) for the "Day" smooth term, degrees of freedom (df), and two estimates of model performance: adjusted R^2 (R^2_{adj}) and the deviance explained by each model (Dev. expl); as these approach 1 or 100% respectively, the model explains more of the variation in the response variable. Null model (denoted $_{NULL}$) presented for comparison in each case, alongside other candidate models (those within 6 AIC units of the lowest AIC model) which are denoted with sequential subscript letters. All models included an intercept term as is standard. Simpler models (e.g. with no site:width interaction or with fewer predictors) did not outperform the final model, so are not presented.

Model ID	s(Day)	Knots	Site	Width	Site:Width	df	AIC	R^2_{adj}	Dev. expl. (%)
GI_{FINAL}	●	6	●	●	●	6.91	-2402.12	0.497	52.8
GI_{NULL}		N/A				2	-6447.52	0	0

Note: parameter estimates and approximate significance of smooth terms are not shown as they do not aid interpretation of the figures given in the main text.

Appendix 2.1.2. Numerical GAM results: Site-specific Gonadosomatic Index

The model shown in Figure 5 (main text) indicates the relationship between GI and day of year across South Devon. Due to apparent differences in the underlying data, the relationship between GI and day of year was also modelled separately for each site (Figure 7, main text; Table A2.2), which appears to indicate a different pattern of spawning condition across the year in Lyme Bay compared to the other sites. The reasons for this are explored in the Discussion (section 4.2), which is supported by the relatively low deviance explained by the model for Lyme Bay compared to other sites (Table A2.2). AIC analysis of these models suggests that variation in GI is not associated with scallop width at any of these sites when considered independently.

Table A2.2. Summary of AIC analyses for site-specific models of gonadosomatic index. Inclusion of the predictor "s(Day)" (smooth term for day of year) is denoted by ●. Other putative predictors (e.g. scallop width) were tested but not deemed important after AIC-based model selection (Appendix 1.3). The final model (denoted $_{FINAL}$) for each site includes only those predictors that were deemed to be significantly associated with variation in the gonadosomatic index. Also shown are the number of knots (curve inflection points) for the "Day" smooth term, degrees of freedom (df), and two estimates of model performance: adjusted R^2 (R^2_{adj}) and the deviance explained by each model (Dev. expl); as these approach 1 or 100% respectively, the model explains more of the variation in the response variable. Null model (denoted $_{NULL}$) presented for comparison in each case, alongside other candidate models (those within 6 AIC units of the lowest AIC model) which are denoted with sequential subscript letters. All models included an intercept term as is standard.

Model ID	s(Day)	Knots	df	AIC	R^2_{adj}	Dev. expl. (%)
Lyme Bay						
Lyme_{FINAL}	●	6	6.91	-2402.12	0.366	39.0
Lyme_{NULL}		N/A	2	-2217.72	0	0
Start Bay						
Start_{FINAL}	●	6	6.98	-3046.09	0.655	67.8
Start_{A}	●	10	9.71	-3048.84	0.659	68.4
Start_{NULL}		N/A	2	-2539.56	0	0
Torbay						
Torbay_{FINAL}	●	7	7.94	-1980.03	0.576	60.1
Torbay_{NULL}		N/A	2	-1713.33	0	0

Note: parameter estimates and approximate significance of smooth terms are not shown as they do not aid interpretation of the figures given in the main text.

Appendix 2.2. Numerical Linear Model results

This section outlines the model selection (AIC analysis for choosing the most parsimonious model) and parameter estimates for the Linear Models which were used to assess predictors of the two measures of scallop maturity: proportion mature (Appendix 2.2.1) and proportion spent (Appendix 2.2.2).

Appendix 2.2.1. Numerical Linear Model results: proportion mature

The proportion of scallops classed as being mature (in maturity stages 5 and 6) was modelled using linear models, and found to vary with day of year, though there was no significant difference in proportion mature between sites (Table A2.3).

Table A2.3. Summary of AIC analyses for District-wide models of proportional maturity (PM). Showing parameter estimates (and standard errors) for the intercept and the predictor "Day" (day of year, and its squared (^{2}) and cubed (^{3}) terms)". Other putative predictors (e.g. Site) were tested but not deemed important after AIC-based model selection (Appendix 1.3). The final model (denoted $_{FINAL}$) includes only those predictors that were deemed to be significantly associated with variation in proportional maturity, based on AIC analyses. Null model (denoted $_{NULL}$) presented for comparison. All models included an intercept term as is standard. Simpler models (e.g. with no cubic Day term) did not outperform the final model, so are not presented.

Model ID	Intercept	Day	Day^2	Day^3	AIC
PM_{FINAL}	0.481 (0.029)	-1.147 (0.223)	-0.649 (0.223)	0.640 (0.223)	-3.708
PM_{NULL}	0.481 (0.038)	N/A	N/A	N/A	24.397

Note: Squared and cubed Day terms allow for a non-linear relationship between day of year and proportional maturity

Appendix 2.2.2. Numerical Linear Model results: proportion spent

The proportion of scallops classed as being spent or recovering (in maturity stages 7 and 3) was modelled using linear models, and found to vary with day of year, with no differences detected between sites (Table A2.4).

Table A2.4. Summary of AIC analyses for District-wide models of proportion of scallops classed as spent/recovering (PS). Showing parameter estimates (and standard errors) for the intercept and the predictor “Day” (day of year, and its squared (^{2}) and cubed (^{3}) terms)”. Other putative predictors (e.g. Site) were tested but not deemed important after AIC-based model selection (Appendix 1.3). The final model (denoted $_{FINAL}$) includes only those predictors that were deemed to be significantly associated with variation in the proportion of scallops classed as spent/recovering, based on AIC analyses. Null model (denoted $_{NULL}$) presented for comparison. Simpler models (e.g. with no cubic Day term) did not outperform the final model, so are not presented

Model ID	Intercept	Day	Day^2	Day^3	AIC
PS_{FINAL}	0.258 (0.021)	1.133 (0.159)	-0.001 (0.159)	-0.622 (0.159)	-42.53
PS_{NULL}	0.258 (0.021)	N/A	N/A	N/A	-2.367

Note: Squared and cubed Day terms allow for a non-linear relationship between day of year and proportional maturity